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Larval Transport and its Association with Recruitment of Blue Crabs to Chesapeake Bay

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The blue crab (*Callinectes sapidus*) harvest in Chesapeake Bay has undergone large yearly fluctuations, creating hardships in the fishing industry and uncertainties in its management. It has previously been suggested that part of the fluctuation may be due to environmental influences during a sensitive period in their life history when blue crab larvae are planktonic outside the bay. During this period, they reside principally in the neuston where wind forced transport has the maximum influence. It is shown, through vector/scalar correlations of wind stress with harvest, that approximately 36% of the harvest variation can be accounted for by the wind patterns during the months from June through September. The influence of alongshore sea level slope and cumulative estuarine discharge (both relating to transport through pressure gradient forcing) on harvest were investigated, but the results were negligible, or ambiguous at best.

Introduction

In this study it is our objective to investigate the degree to which coastal transport (identified through the forcing terms: wind stress, alongshore sea level slope and estuarine discharge) can be related to recruitment success (identified by the harvest) of Chesapeake Bay blue crab (*Callinectes sapidus*).

Harvest of the Chesapeake Bay blue crab had undergone large yearly variations, creating unstable conditions in the dependent fishing industry and making it difficult to optimize the yield through effective management. In part, successful management depends on the ability to identify those factors (both biotic and abiotic) which dominate population dynamics of the stock, and on the ability to separate controllable factors (such as harvest pressure) from non-controllable factors (such as environmental conditions). Furthermore, there is the obvious need to predict future effects of present environmental conditions in order to adequately prepare for the harvest.

Previous work has suggested that variability of oceanic transport during critical planktonic larval stages of the blue crab, outside the estuarine nursery grounds, may be

partly responsible for the variations in year class sizes in Chesapeake Bay (Johnson *et al.*, 1984). But ocean transport, itself, is the result of complex forcing, and recruitment success to juvenile stocks may be far removed from harvest success of adults. In this study we relate harvest to several environmental forcing factors using vector and scalar correlations. However, rather than approach the problem as a statistical exercise, we explore a hypothesis that has been in development for several years. In the first part of this paper, an outline is given of our present understanding of blue crab reproductive strategy in Chesapeake Bay along with a discussion of field and theoretical investigations of the dispersion of larvae outside the bay. Secondly, a presentation is made of the vector/scalar correlation method and a summary is given of its use in the analysis of environmental forcing. Finally, the results of statistical examination of the hypothesis are presented.

Background

Callinectes strategy

The reproductive biology of *Callinectes sapidus*, the blue crab of Chesapeake Bay, has been described by Cronin *et al.* (1957), Van Engel (1958) and Tagatz and Hall (1971) among others. A synopsis of blue crab biological data, along with an extensive bibliography, can be found in Millikin and Williams (1984).

After mating, the Chesapeake Bay blue crab females migrate to the higher salinity waters near the bay entrance where spawning takes place on an ebb tide, assuring that the larvae are deposited in the open ocean environment of the continental shelf. Spawning occurs between May and early September, reaching maximum in late July (McConaughy *et al.*, 1983; Van Engel, 1958). Development includes eight zoeal stages and a megalopa stage that reaches metamorphosis approximately 40 days after hatching (Costlow & Bookhout, 1959).

Growth is rapid, larvae hatched in the spring become adults in August of the following year. Those hatched during peak spawning reach maturity in the spring of the third summer (Van Engel, 1958). Crabs live at least a year past reaching adulthood, with the maximum lifespan estimated to be three to three and a half years. Hence, crabs that hatch during a given summer may contribute to the harvest for the subsequent three summers, with the largest contribution made by two-year olds. Historically, post-spawning crabs were thought to move to deeper waters of the bay, or to the ocean, where they died or joined an ocean population that returned to the bay as 'ocean' crabs the following year. Recent modelling of the population dynamics suggests that in order to maintain a harvestable population in the bay, females may mate and spawn more than one season (Hester, 1983).

Larval dispersion

Several biological studies have indicated that spawning behaviour of Chesapeake Bay blue crab seems designed for ejection of larvae seaward from the bay entrance. Provenzano *et al.* (1983) investigated the diurnal vertical distribution of the first stage larvae in the bay mouth and found that larvae are hatched synchronously just prior to maximum ebb tide. Immediately rising to the neuston, these larvae are transported offshore in the ebb flow.

McConaughy *et al.* (1981) examined the horizontal distribution of blue crab larvae in the bay entrance and surrounding shelf waters. Early stages and post-larvae (megalopae) were found in the bay mouth, while intermediate stages were detected at offshore stations. Maximum abundance (85%) of all stages were found in the upper meter of the water

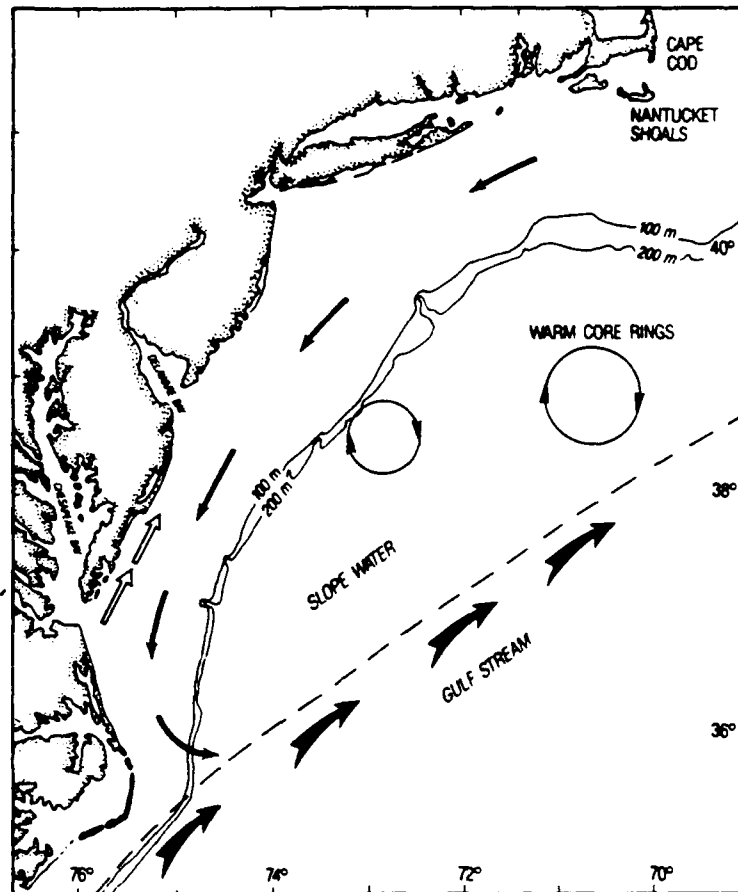


Figure 1. General circulation schematic of the Northwest Atlantic showing the relationship of the southward flow along the Middle Atlantic Bight to the Gulf Stream and to the inshore wind drift during summer.

column where wind forced transport is optimum. Epifanio *et al.* (1984), investigated the distribution of blue crab larvae around the entrance to Delaware Bay, finding a similar pattern, and suggesting a similar cycle of environmental involvement.

A physical mechanism for the retention of the larvae within sufficient proximity to the bay entrance for reinvasion at the appropriate time has been proposed by Johnson *et al.* (1984). A poleward pressure gradient along the Middle Atlantic Bight gives rise to an equatorward drift. If the larvae were caught up in this drift, they would be transported toward Cape Hatteras and lost from Chesapeake Bay (Figure 1). However, during June, July and August (peak spawning months), the wind stress is consistently toward the northeast quadrant—in September, it is southwestward (Figure 2). In shallow, nearshore water, the influence of the alongshore pressure gradient and the cross shelf density gradient is diminished, and the effect of wind stress becomes dominant (Johnson *et al.*, 1984). Away from the near-field dynamics of the bay mouth, then, it seems likely that in July and August, a region of poleward flowing water (wind forced) exists between the shoreline and mid-shelf southward flow (pressure gradient forced).

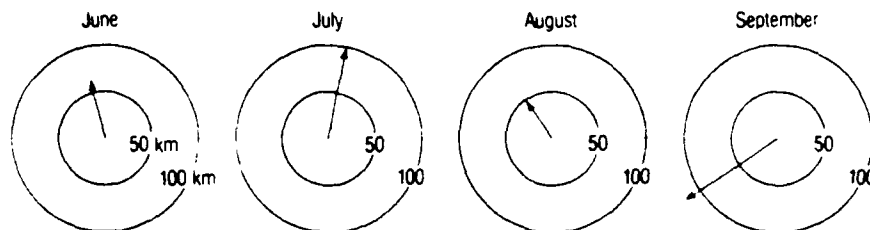


Figure 2. Advective length scale derived from averaged wind stress measurements at Norfolk, VA, airport from 1952 through 1980. The scale is obtained from surface wind drift currents, $u_s = 0.55 (\tau / \rho_a)^{1/2}$, where ρ_a is air density, τ is wind stress and u_s is estimated drift.

During July and August, larvae are most likely advected from the bay in the southeast direction with outflowing surface water (Boicourt, 1973). When the outflow intensity is diffused, the effect of wind stress becomes dominant, and the larvae are carried poleward. The existence of this wind influenced nearshore zone permits the larvae to be retained in the area with reasonable access to the bay. Toward September, the larvae have developed to the megalopal stage, and the wind stress shifts toward the south/southwest, appropriate for aiding in the reinvasion (Johnson *et al.*, 1984).

An example of the wind effect on surface waters near Chesapeake Bay is presented in Figure 3: A line of Rapid Boundary Current Meters (Johnson, 1987b) measured surface currents across the immediate outflow region of the bay during a period of wind stress toward the northeast. Although the outflow water first bends toward the southeast, in alignment with the channel direction, wind stress rapidly turns this flow toward the northeast. Lagrangian drifters, release in the bay's entrance during the same period, confirmed the northeastward flow (Boicourt *et al.*, 1987).

Indirect evidence of wind influenced transport in nearshore waters of the Chesapeake Bight has been given by tracing backward from where large quantities of blue crab megalopae were found offshore, to their (predicted) point of origin. In Johnson (1985) and Johnson (1987a), measured winds were applied to a model of surface currents in order to develop a pseudo-trajectory of larval dispersion. Figure 4 gives several examples of the results of this method demonstrating the complex history of the traces (due to the variable winds) and confirming their origin, their length of time for development to the megalopae stage outside the bay, and the significant influence of wind stress in transporting the larvae.

If recruitment of megalopae to the bay is dependent on transport in the wind-controlled nearshore zone, the supply of adult blue crabs for bay fisheries would also be affected by variations in the yearly pattern and strength of the winds during the critical time that the larvae are offshore. Hester (1983) modelled the dynamics of the bay's blue crab population as exponential depletion of the cohorts of a population with replacement through reproduction. Wind stress was incorporated as a mechanism influencing larval recruitment success and the subsequent strength of the cohort in the harvest. Although a wind index (derived from a component of the wind blowing parallel to the coast) did describe the major peaks in the harvest of about 5 year cycles, the low frequency trend in the curves did not relate well.

Environmental conditions in the Chesapeake Bight have been investigated more thoroughly in subsequent papers (Johnson, 1985—wind forced dispersion; Leming &

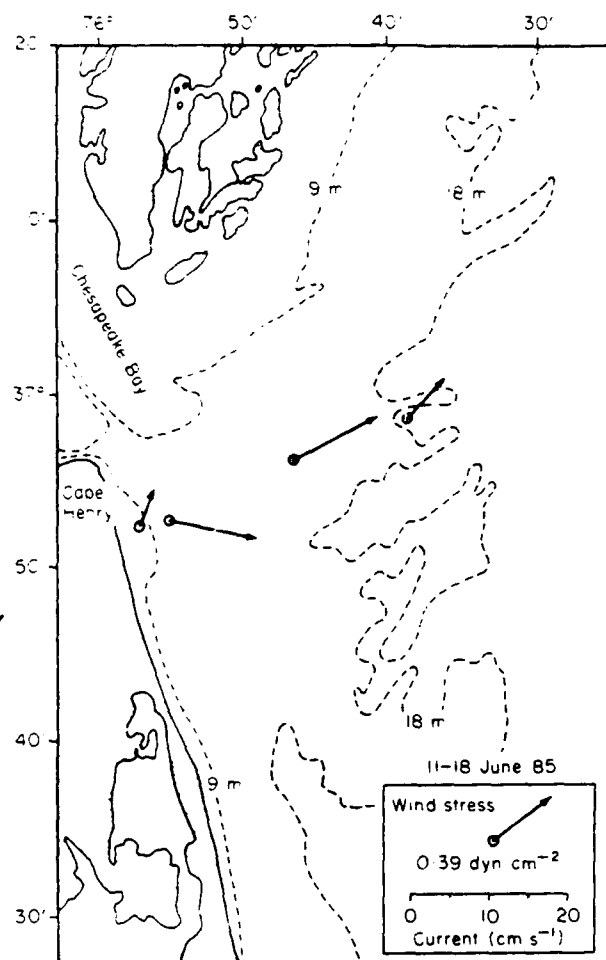


Figure 3. Measured surface currents immediately outside Chesapeake Bay. Bay discharge is toward the southeast. Wind stress during this time is shown in the lower righthand box. Note the effect of wind stress in turning the surface current toward the northeast.

Johnson, 1985—circulation models; Johnson, 1987a—nearshore surface currents). In the present study, an attempt is again made to relate yearly harvest variation to yearly wind stress variation, but in this case we will approach the problem with the aid of vector/scalar correlations.

Approach

Complex correlation

Complex (vector) correlation methods have been successfully used in several oceanographic applications. Kundu (1976) provides a good description of the method and its application to ocean current vectors. Although vector/scalar correlations (e.g. wind stress versus harvest) follow the same mathematical principals, the methods of relating vectors

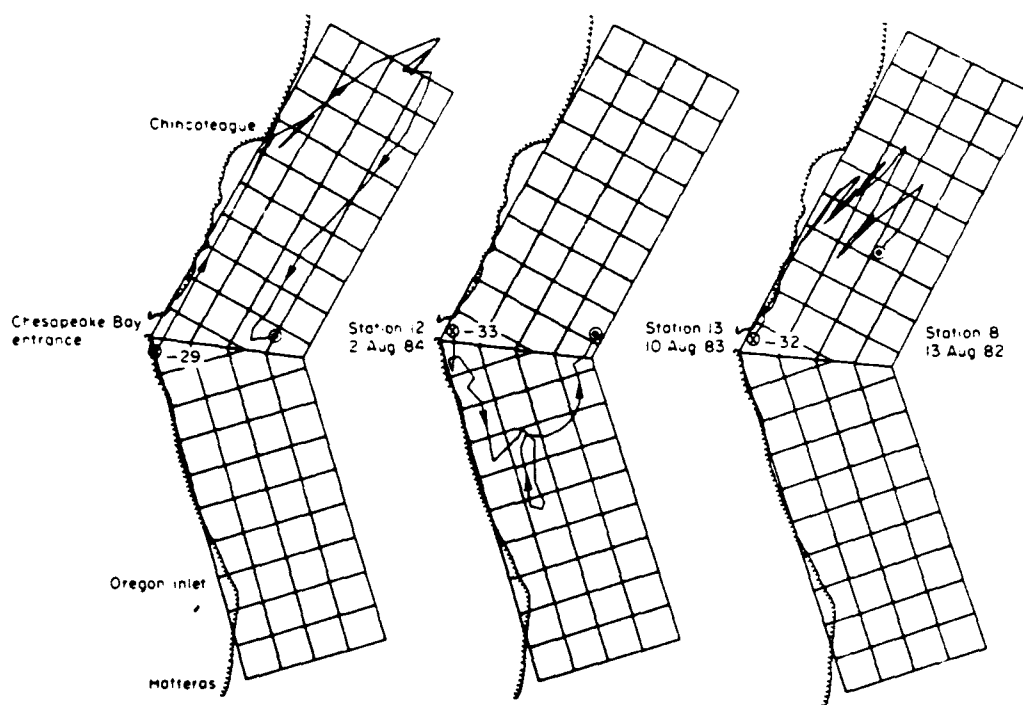


Figure 4. Examples of modeled back-traces from locations where blue crab megalopae were found (⊙) to approximate spawning location (⊗). Arrows indicate direction of drift. Negative numbers represent calculated days backward from date of sampling. Grids are 10 × 10 nm. Note complex history of traces due to variable winds. From Johnson (1987a).

and scalars have tended, rather, to involve separate correlations of the scalar with a component (scalar) of the vector. For example, the Ekman Index (component of wind stress parallel to the coast divided by the Coriolis parameter) has been commonly related to sea surface temperature in order to quantify the effect of wind stress on upwelling. However, due to complex relationships between circulation and wind forcing in coastal waters, the most effective upwelling wind stress direction may be at some angle to the coast.

From Figure 5 and the following definitions, vector scalar correlations can be easily understood:

$u, v \equiv$ (east, north) components of wind stress,

$\omega \equiv u + iv$,

$\omega^* \equiv u - iv$ (complex conjugate of ω),

$i \equiv \sqrt{-1}$,

$s \equiv$ scalar value (e.g. harvest magnitude),

and

$\langle \rangle \equiv$ expected value.

Referring to Figure 5, the scalar value with its mean removed (e.g. yearly harvest magnitude variation) is assigned to the real axis (positive is east pointing). In this sense, then, it is a vector assigned only to the real axis, with temporal variations in the length and direction

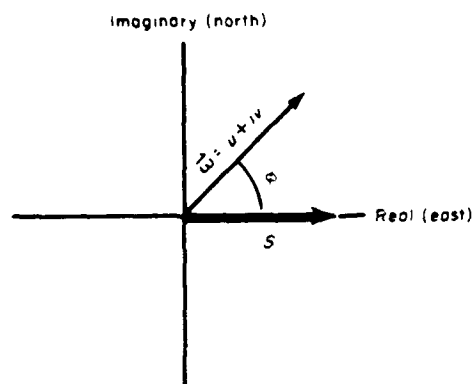


Figure 5. Coordinate system for vector-scalar correlations. S represents the scalar data, with values along the real axis only. \bar{w} is the vector, with values traced out in the imaginary plane by the head of the vector. ϕ represents the direction of correlation with respect to the real axis.

(negative toward the west) of this pseudo-vector describing yearly variations in the scalar magnitude. Correlation between the vector, with its mean removed (e.g. wind stress variations), and this pseudo-vector is given as,

$$\bar{R} = \frac{\langle \omega s \rangle}{\langle \omega \omega^* \rangle^{1/2} \langle s^2 \rangle^{1/2}} \equiv a + ib$$

$$a = \frac{\langle us \rangle}{\langle u^2 + v^2 \rangle^{1/2} \langle s^2 \rangle^{1/2}}; \quad b = \frac{\langle vs \rangle}{\langle u^2 + v^2 \rangle^{1/2} \langle s^2 \rangle^{1/2}}$$

$|\bar{R}| = (a^2 + b^2)^{1/2}$ correlation magnitude,

and $\phi = \text{Arctan}(b/a)$ correlation direction.

The direction, obtained in this fashion, is the angle between the positive real axis (positive increase in the scalar value) and the correlated vector. This mathematical representation of direction (counter-clockwise from east) is easily converted to a geographical direction (clockwise from north). In the following data analysis, all directions are given as geographical directions. The statistical significance of the direction is directly related to the statistical significance of the correlation magnitude, e.g. when the correlation is significant, the direction is also significant.

Data sources and treatment

Blue crab harvest data have been extracted from Current Fisheries Statistics, Annual Summaries for Chesapeake, Maryland and Virginia Landings, produced by the National Marine Fisheries Service for the years 1952 through 1980. Statistics are derived from landings for the Virginia portion of the bay by the Virginia Marine Resources Commission. In the Maryland portion of the bay statistics were obtained by a mailing census prior to 1980. In 1981, Maryland significantly altered their procedure, resulting in a nearly 100% increase in reported size of the harvest over the previous method. Although we attempted to create a comparable statistic for Maryland for the years following 1980 by ratio with the Virginia statistic, we were left with an uncertainty of about $\pm 20\%$, which is too significant to ignore.

Our time series of harvest data then consists of the total yearly landings in pounds for the years 1952 through 1980 (29 points), and includes both Virginia and Maryland portions of the bay and Virginia coastal waters.

Wind measurements were taken at Norfolk, Virginia, airport, with an anemometer mounted at 10 m height (data available through the National Climate Center, Asheville, NC). Unbroken records were available for 29 years, from 1952 through 1980. Wind stress components were calculated from hourly and 3-hourly records, using a drag coefficient of $\rho_a C_D = 2 \times 10^{-6} \text{ g cm}^{-3}$. Monthly averages of the components were formed for the months of June, July, August and September, the principal months of larval dispersion and recruitment, and a time series created for each month over the 29 years. The means were subtracted from the four time series.

Although a concern must be expressed for the inland location of the anemometer and its representativeness for winds in the Chesapeake Bight, it is felt that the long, unbroken record, the relatively flat terrain surrounding the anemometer, and the care taken in obtaining and processing the data make it a particularly useful data set. We suggest, without proof, that the low frequency content (monthly averages) of the resulting wind stress time series removes much of the space/time ambiguity between land and sea based sampling sites.

Sea level data were obtained for tide stations located at Sandy Hook, NJ, and Kiptopeke, VA (NOAA/NOS: Hicks *et al.*, 1983). Monthly averages of hourly height were made, and an alongshore sea level difference generated by subtracting the height at Kiptopeke from the height at Sandy Hook. In the remainder of this paper we will be referring to this difference as the sea level slope, since the station separation enters as a constant and is not significant to the correlations. Positive slope is toward the northeast. Again, four time series were made for the months of June, July, August and September for the years 1952 through 1980, and the means removed from each series.

A measure of estuarine discharge was obtained from estimated cumulative streamflow entering Chesapeake Bay. The estimated streamflow is obtained from measurements in each of the rivers flowing into the Bay, and the sum of the contributions from all of the rivers provides an estimate of discharge at the entrance (Section E from USGS newsletter: A monthly summary of cumulative streamflow into the Chesapeake Bay; USGS, Towson, Md.). It is important to note, however, that this is not given as a true measure of instantaneous discharge from the bay since flow from rivers emptying into the upper bay may not reach the entrance until one or two months after the measurements, with no account being taken of the (poorly known) time delay between river flow and its arrival at the entrance.

In this study, we use the streamflow data as a measure of the quantity of accumulated fresher water in the coastal zone and, by implication, an estimate of the cross shelf density gradient variation. For this purpose then, the streamflow across Section E (bay entrance) is summed for four months during the spring of each year (March, April, May and June) to provide a time series of estimated yearly variation in accumulated coastal low salinity water. The mean is removed from the series. The interesting, and probably important, instantaneous discharge rate of Chesapeake bay cannot be addressed here.

Results

Wind stress and sea level slope

Although the ambient alongshore sea level slope in the Middle Atlantic Bight is considered to have origins in basin scale dynamics (Hopkins, 1982; Beardsley *et al.*, 1976), it

TABLE 1. Correlation of wind stress with sea level slope between Kiptopeke Beach, VA and Sandy Hook, NJ. Where r is the correlation magnitude and ϕ is the correlation direction (geographic)

Month	r	ϕ
June	0.30	36
July	0.39	42
August	0.57	41
September	0.47	22

TABLE 2. Correlation of estuarine discharge with harvest. Discharge represents cumulative river flow from March through June at Section E (see text). Harvest has been lagged from 1 to 3 years behind the discharge measurements

Year lag	r
1	-0.16
2	0.01
3	-0.10

can be expected that variations in alongshore wind stress will contribute to variations in this slope. In particular, it is reasonable to expect that a northeastward, alongshore wind stress will produce a positive sea level slope (rising toward the northeast), and a southwestward wind stress will produce a negative sea level slope, i.e. correlations between the two time series should result in a correlation direction toward the northeast.

Table 1 shows the results of correlation between wind stress and sea level slope for the four summer months. July, August and September correlations (0.39, 0.57 and 0.47, respectively) are at the 95% confidence level for significance (rejecting the null hypotheses); June (0.30) is at the 88% level; and the directions are all toward the northeast. This result is in accord with our expected notion that when the wind stress acts toward the northeast along the coast, the sea level rises in that direction; hence, the results from vector/scalar correlations for this simple exercise tend to confirm the method.

Harvest and estuarine outflow

As previously stated, the estuarine outflow time series that is used here may more properly be described as an estimation of the pooling of fresher water along the coast. It is a rough measure of the cross self density gradient variation which, in turn, is related to alongshore geostrophically balanced flow. In Table 2, the results of simple scalar/scalar correlations of the crab harvest at lags of 1, 2 and 3 years with outflow are presented. The lags reflect the time delay between environmental effect on a larval year class and the involvement of that year class in the harvest.

It is clear from Table 2, that there is no significant correlation between outflow and harvest. Although it was felt that this result should be presented here for completion, it cannot be considered to be a fair representation of the effects of outflow on population dynamics. Lacking long time series of instantaneous outflow measurements or of actual

TABLE 3. Correlation of harvest with wind stress (left) and with sea level slope (right). The harvest has been lagged by two years behind each series.

Month	Wind stress		Sea level slope
	r	ϕ	r
June	0.25	12°	-0.05
July	0.20	333°	-0.06
August	0.29	40°	0.20
September	0.23	202°	0.21

TABLE 4. Correlation of harvest with a composited wind stress vector consisting of the vector addition of June, July, August and negative September wind stress.

Year lag	r	ϕ
1	0.38	18°
2	0.46	18°
3	0.20	17°

Correlation of harvest with composited (as above) and weighted wind stress [$0.25 \times \text{year (1)} + 0.50 \times \text{year (2)} + 0.25 \times \text{year (3)}$]

r	ϕ
0.60	18°

cross shelf density gradients, their possible influence on the larval transport and recruitment must be considered to remain uncertain.

Harvest, wind stress and sea level slope

Table 3 shows the results of vector/scalar correlation between wind stress for each month (June, July, August and September) and harvest; and of simple scalar correlations between sea level slope for each month and harvest. It should be noted that this table demonstrates the results of a statistical exploration to determine the separate influence of the individual months on the harvest; the actual harvest would necessarily result from the summed contributions. For this reason, the correlations are only *marginal*. Nevertheless, the correlated directions definitely demonstrate the pattern of our conceptual model: transportation of larvae toward the northeast during the summer months and back toward the southwest in September (the July correlated direction is actually toward the northwest, but the correlation magnitude is weakest, giving more uncertainty in the direction). Recognizing that two-year old crabs dominate the harvest, the correlations in Table 3 were made with a two year lag between wind stress and harvest.

The correlations shown in Table 3 between sea level slope and harvest are ambiguous: for the June and July time series, the correlations are nearly zero; and for the August and September time series, the correlations are both positive, but marginal at best. However,

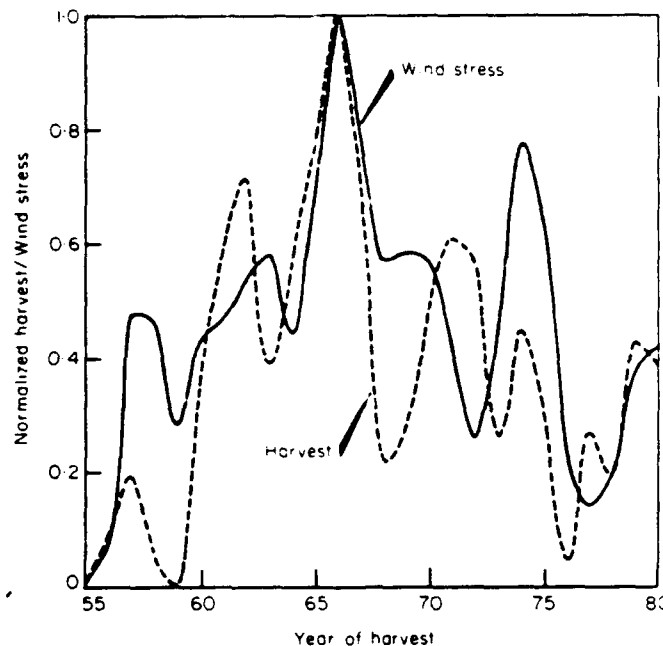


Figure 6. Comparison of the harvest record of blue crabs with the composited, filtered wind stress vector (see text). The minimum value has been subtracted from each series and the remainder normalized such that the series runs between zero and one.

from our conceptual model, it should be expected that the correlation would be negative in August, with an increase in harvest resulting from an increased transport toward the northeast (negative sea level slope), and positive in September (transport toward the southwest).

It was shown in the previous paragraph that a significant relationship exists between the sea level slope and wind stress. Part of the problem with sea level slope may be that the measurements are dominated by local sea level set-up and set-down due to wind stress in the neighborhood of the tide gauge. Rather than representing a direct influence on larval transport, sea level measurements may, then, just indirectly reflect the relationship between wind stress and harvest.

Composited wind stress and harvest

Although the relationship between sea level and harvest appear to be ambiguous and will not be pursued further, the relationship between wind stress and harvest as shown in Table 3 is highly encouraging. Since each month contributes additively to the harvest population, a new vector series was created by vectorially adding the wind stress for the months of June, July and August (correlated toward the northeast), and subtracting the September wind stress (correlated in the opposite direction). This new, composited wind stress vector series was correlated with harvest at one, two and three year lags, again reflecting the time lag between the environmental influence on larvae and their influence on the harvestable population. The results are greatly improved, as shown in Table 4.

Referring to Table 4 (upper), the two year lag series have the highest correlation, in agreement with the fact that two-year-old crabs dominate the harvestable population.

Both the one and two year lag correlations are significant at the 95% level. The third year correlations are only marginal. Although it is thought that three-year-old crabs are represented in the population, the diminished correlation magnitude may reflect the influence of harvest on this year class prior to reaching this age. In all three years the composited correlation vector points toward the north northeast as expected from the conceptual model (recalling that September wind stress was subtracted from the series).

Finally, we form a composited and filtered wind stress vector series by weighting the composited wind stress vector for each year class by the expected relative contribution of that year to the harvest in any given year. The two year class is weighted by 0.5, and the one and three year classes are weighted 0.25. It is easily recognized that the convolution of these weights with the composited wind stress vector series represents the commonly used hanning cosine filter. Besides reflecting the relative contribution of the year classes, this hanning filter has the useful attribute of reducing sampling frequency (Nyquist) error. Although it is tempting to weight each year class by the relative correlation magnitude as presented in Table 4 (upper), such an uneven filter would tend to skew the spectral content of the series.

The result of correlating harvest (lagged by two years) with the composited and weighted wind stress vector series is presented in Table 4 (lower). The direction of the correlated vector is toward the north/northeast as expected, and the correlation magnitude has risen to the surprisingly large value of 0.60.

In order to view the relationship, each series was chopped and normalized so that it varies between 0 and 1, and the resulting time series presented in Figure 6. Referring to Figure 6, it can be seen that the wind stress vector series contains the major curve of the harvest (peak in 1966) and indicates the presence of the *c.* 5 year cycle. It is suggestive that some of the one-year misalignment in peaks of the *c.* 5 year cycle may be due to smearing caused by uncertainty in contribution levels of the three (year) classes to the harvest.

Summary and discussion

Female blue crabs migrate down Chesapeake Bay and spawn in the entrance during ebb tide; the larvae are immediately ejected from the bay, spending the next 30–40 days in the neuston of continental shelf waters before recruitment back into the bay occurs. Since the ambient flow in the Middle Atlantic Bight is principally toward the south, the larvae would be transported away from the vicinity of the bay and unable to reenter at the appropriate time were it not for wind stress forcing in the shallower coastal region of the shelf.

During the principal spawning months of June through August, wind stress is toward the north and northeast, counteracting the ambient flow induced by pressure gradients. During September, when the larvae are ready for recruitment, the wind stress swings toward the southwest. Our working hypothesis has been: that the life history strategy of the blue crab is related to relatively consistent environmental conditions in shelf waters which aid in dispersion of larvae, and retention in the area for later reinvasion of the bay; that if variations occur in the environmental conditions during this sensitive time, it would affect the population of that year class in the bay.

Using vector/scalar correlations between wind stress and later harvest levels, a significant correlation of 0.6 was found, with a correlation vector along the north/northeast orientation as expected from the conceptual model of dispersion and recruitment. The

wind stress time series for this correlation took into account the accumulative vector contribution of winds blowing toward the northeast during June to August, and toward the southwest during September. In addition the correlation took into account the contribution from one-, two- and three-year-old age classes, with domination by the two-year-old age class.

It was somewhat surprising to find that wind stress induced larval transport, during a relatively short period in the life history of the blue crab, accounts for 36% of the harvest variation (r^2). This result tends to emphasize the fact that sensitivity to environment is a complex function of the species strategy, and is not easy to unravel without a well identified conceptual model.

Such a strong relationship was also unexpected because of the assumption that had been made relating harvest level to population size. Clearly, harvest statistics are subject to vagaries of sampling; economics play a role in determining the harvest intensity; and harvesting techniques over the years have somewhat varied. In addition, there has been no consideration of growth rate and survivability during juvenile stages within the bay. On the other hand, the working hypothesis was established upon a model with strong definition; and the large size of the harvest in Chesapeake Bay tends to reduce statistical vagaries.

One final comment must be made on the role of estuarine discharge. Although no correlation was found between 'pooling' of fresher water in the coastal region from cumulative discharge and harvest level, it is felt, without specific proof, that initial dispersion away from the bay and recruitment back into the bay must be felt in larval success rates. Further efforts at monitoring instantaneous estuarine discharge and subsequent interactions with shelf waters would be helpful.

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